(Temporary...) Overlooked model uncertainties may misinform forest management strategies

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ABSTRACT

Climate change poses significant challenges to forest management in Europe, where rising temperatures and increased frequency of extreme weather events threaten forest health and productivity. Thus, policy makers and forest managers urgently need robust projections of the suitability of future climatic conditions for5 forest tree species to guide conservation efforts, forest management strategies and make informed decisions. Previous studies, which aimed at providing such projections, mostly made use of a single type of model to do so (correlative models) and failed evaluating the uncertainties associated with the model projections. Here, we simulated the distribution of six European tree species over the 21st century, using various correlative and process-explicit models and the most recent climatic projections (SSP2 and SSP5 scenarios). We examined several versions of the models differing by their complexity and calibration methods in order to identify and quantify the different sources of uncertainty in their projections. We find (i) that the use of occurrence data to calibrate models, whether correlative or process-explicit, consistently leads to more pessimistic predictions, and (ii) that using different modelling approaches together allow to assess more rigorously projection uncertainties. Evaluating and communicating the degree of uncertainty enhances the credibility of species distribution models, and contributes to a better adaptation to the impacts of climate change on forest ecosystems.

Introduction

Forests are increasingly under pressure from climate change. In Europe, where temperatures are rising twice as fast as the global average (Copernicus Climate Change Service, 2024), unprecedented pulses of tree mortality were reported in the last decade (Senf et al, 2020). These damages are observed not only in populations living at the margins of their climatic range, but also in those living in the core of their range. Some European forests have even become net CO2 sources recently in some areas (Hadden and Grelle, 2016; Karelin et al, 2021), due to decreased growth (Hadden and Grelle, 2016; van der Woude et al, 2023), increased burned areas (Carnicer et al, 2022; Kelly et al, 2024), and increased dieback driven by increased drought frequency and intensity and increased vulnerability to pest attacks (Cienciala and Melichar, 2024; Karelin et al, 2021; Latifovic and Arain, 2024).

Forests have nevertheless a major role to play in mitigating climate change and achieving carbon neutrality (Hyyrynen et al, 2023; Korosuo et al, 2023). Forests managers are facing unprecedented short-term and long-term challenges, as they need to address current dieback issues while promoting forest adaptation to climate

change. These decisions have to be made in a context of high uncertainty, because of the lack of data and knowledge about the effects of climate change, interacting with various forest management strategies.

While long-term experiments yield unique insights into biological processes at stake, predictive ecological models are essential to complement and extend them by examining the drivers operating at large spatiotemporal scales (Levins, 1993; Mitchell and Dietrich, 2006). Some of these models aimed at identifying, at the regional or continental scale, which species will be able to grow in future climatic conditions. Most studies project pronounced species range shifts and forest composition changes in Europe. Deciduous late-successional species, mostly oaks (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica* L.), are expected to expand their range towards North-eastern Europe and decline in France (Dyderski et al, 2018; Hanewinkel et al, 2013; Hickler et al, 2012; Saltré et al, 2015; Schueler et al, 2014; Takolander et al, 2019; Wessely et al, 2024). Areas suitable for Mediterranean oak forests, including for evergreen oak, should increase (Hanewinkel et al, 2013; Ohlemüller et al, 2006; Takolander et al, 2019). On the contrary, coniferous trees, such as spruce (*Picea abies* L.) or pine (*Pinus sylvestris* L.), may loose large portions of their current range (Hanewinkel et al, 2013; Schueler et al, 2014; Wessely et al, 2024). These climate-induced species shifts are predicted to have major impacts on timber production and forest economic sector (Hanewinkel et al, 2013; Wessely et al, 2024).

However, there is often considerable uncertainty associated with the future trajectory of ecosystems. Model projections are subject to many sources of uncertainty, whether they are correlative species distribution models (CSDMs) or process-explicit models (PEMs). Most studies have relied on correlative approaches, and, when the uncertainties were addressed (which is not at all systematic; Simmonds et al, 2024), they primarily focused on three sources of errors: the data quality used for model fitting (Barbet-Massin et al, 2010; Chen et al, 2013; Duputié et al, 2014; Faurby and Araújo, 2018), the variation among climate change projections (Beaumont et al, 2007; Diniz-Filho et al, 2009; Thuiller et al, 2019), and the variation among modeling method (Diniz-Filho et al, 2009; Pearson et al, 2006; Thuiller et al, 2019). The latter often only corresponds to the fitting algorithm (GLM, GAM, Random Forest...). Even though the differences between these algorithms can be significant, previous studies are still far from encompassing the diversity of modeling approaches that exist (Dormann et al, 2012). They thus ignore a large part of the methodological uncertainty of the projections. This is a major shortcoming, especially since process-explicit models might be more robust under novel climatic conditions (Van der Meersch et al, 2024; Chapter 2).

The handful of studies that have compared CSDMs with PEMs have shown that their projections indeed significantly diverge in future climatic conditions (Cheaib et al, 2012; Keenan et al, 2011; Morin and Thuiller, 2009; Takolander et al, 2019), and PEM projections tend to be more nuanced. These studies have provided some essential insights, though they were limited to a qualitative comparison of projections over a limited area and did not account for climatic uncertainties (i.e. they used a single climate model). Today, it is nev-

ertheless essential to quantitatively understand how the different approaches of species distribution models influence the uncertainty of projections, considering the interaction with the climate, and how these uncertainties will evolve over time.

Understanding where do the uncertainties originate and and how they relate to each other is indeed a critical challenge. From the modeler point of view, it is obviously crucial to identify opportunities for model developments (Petchey et al, 2015). But it has broader implications beyond the scientific community, to address policy-relevant questions (Urban et al, 2016). Clarifying and quantifying the many uncertainties that the different actors will face in the 21st century supports the development of robust and sustainable forest management practices that can accommodate a range of possible future scenarios (IPCC, 2021). In particular, it helps identify how serious the risk is for the forest considered, and if any action is required. Forest managers need to know whether the current species will be able to tolerate future climate conditions, whether they can rely on its natural regeneration, or whether they should capitalize on new species opportunities. It is not reasonable to ignore these uncertainties or to consider only a portion (e.g. omitting model methodological uncertainty) if we aim to secure the capacity of Europe's forests to continue providing ecosystem services.

To capture the full breadth of uncertainties that are relevant to assess how climate change will affect forests across Europe, we simulated the future distribution of six tree species (*Abies alba* Mill., *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., *Quercus pubescens* Willd. and *Quercus ilex* L.) with different modeling approaches, using 10 different climate projections (5 global climate models and 2 socioeconomic scenarios) from the CMIP6 dataset (Noël et al, 2022). We then used an ANOVA-based variance decomposition to identify the different sources of uncertainty and quantify their relative contribution to the total projection uncertainty.

Methods

Species distribution models

We sought to encompass the greatest diversity of species distribution modeling (SDM) approaches by including three different approaches, along the correlative–process spectrum (Dormann et al, 2012): correlative models (CSDMs), process-explicit models (PEMs) and fitted PEMs (hybrid approach between CSDM and PEM).

For the correlative approach, we selected five well-established models following the performance comparison by Valavi et al (2022): GLM with lasso regularization, GAM, BRT, MaxEnt and down-sampled Random Forest. We selected a set of uncorrelated climate predictors, based on their implicit relevance for tree species: minimum temperature of the coldest month (representing frost tolerance), total precipitation (representing available water), GDD5 (growing degree days >5°C) between April and September (representing available thermal energy for vegetation growth and fruit maturation), and water balance between June and July (difference of precipitation and evapotranspiration, representing summer drought tolerance). We also included two soil covariates (pH and Water Holding Capacity). We calibrated the models using species occurrences from the dataset assembled in Van der Meersch and Chuine (2023), mostly based on EU-Forest inventory data (Mauri et al, 2017), and 50,000 background points (to properly represent the full range of environmental conditions across Europe, Valavi et al, 2022). For each model and each species, we ran a fivefold environmental cross-validation to estimate model performance in novel extrapolation conditions (Roberts et al, 2017). We then used all the available training data to calibrate the models in order to favour final prediction quality (Roberts et al, 2017).

For the process-explicit approach, we used the model PHENOFIT. It assesses the fitness of an adult tree by simulating the precise phenology (leaf unfolding, flowering, fruit maturation, leaf senescence), and damages caused by abiotic stress (frost, drought) relatively to the development stages of the different organs. The parameters of PHENOFIT are either calibrated with direct measurements, literature data, or inferred using observations of the processes modelled (e.g. species-specific phenological dates to calibrate phenological subcomponents). Its calibration thus does not involve species occurrence data. PHENOFIT requires daily climate variables, as well as the soil water holding capacity. The model has been validated for several North American and European species, either in historical or Holocene climatic conditions (Duputié et al, 2015; Gauzere et al, 2020; Van der Meersch et al, 2024; Morin et al, 2007; Saltré et al, 2013). This modeling approach will be referred to as *expert* PEM in the following.

We also included a fitted PEM, somewhere in the middle of the correlation–process continuum (Dormann et al, 2012). To this aim, we calibrated PHENOFIT using species occurrence data as CSDM do, with the constraints of the model's process-explicit structure. We optimized the parameters of the model using the covariance matrix adaptation evolution strategy (CMA-ES, (Hansen and Ostermeier, 2001)), on a multicore

cluster, following Van der Meersch and Chuine (2023). To reduce the computational cost of this inverse calibration, we calibrated the model with subsets of 2000 points (1000 presences and 1000 absences), from the same dataset as correlative models (see above). We calibrated 10 times each species parameter set, with five repetitions on two random subsets of presences/pseudo-absences (except for beech, for which we ran 10 repetitions on 10 subsets).

The three modeling approaches output a variable between 0 and 1, indicating how well the climate is suitable for the species. This suitability index can be converted into a binary predictor, with a threshold that maximizes the true skill statistic (TSS, calculated from a confusion matrix).

The robustness of these three different approaches was assessed by hindcasting the range shifts of five forest tree species across Europe over the last 12,000 years (Van der Meersch et al, 2024; Chapter 2). The results indicated that the transferability of PEMs (either expert or fitted) was higher in climates that were significantly different from the historical period.

Finally, for beech only, we also included a *partially* fitted PEM. It was calibrated in the same way as the fitted PEM, but we optimized only some critical parameters that were identified as responsible for errors in the expert PEM simulations (Chapter 3). Other parameters were fixed at the expert values. Note thas this partially fitted PEM was not included in the uncertainty partitioning (see below).

Environmental data

CSDMs and fitted PEMs were calibrated with historical climatic conditions (1970-2000) from ERA5-Land dataset at a 0.1°resolution (Muñoz-Sabater et al, 2021). Soil data were extracted from EU-SoilHydroGrids (Tóth et al, 2017) and SoilGrids (Hengl et al, 2017) databases.

Future simulations were run with the last Coupled Model Intercomparison Project Phase 6 (CMIP6) climate projections, for 5 global climate models (GCMs) and 2 shared socio-economic pathways (SSPs). Model projections were downscaled to a 0.1° resolution with a statistical trend-preserving method (the cumulative distribution function transform), using the ERA5-Land reanalysis as a reference observational dataset between 1981 and 2010 (Noël et al, 2022). The five GCMs were GFDL-ESM4 (Dunne et al, 2020), IPSL-CM6A-LR (Lurton et al, 2020), MPI-ESM1-2-HR (Müller et al, 2018), MRI-ESM2-0 (Yukimoto et al, 2019) and UKESM1-0-LL (Sellar et al, 2020). They are considered as good representatives of the full CMIP6 ensemble (Noël et al, 2022). We selected scenarios SSP2-4.5 and SSP5-8.5, because the projected total cumulative CO2 emissions according to two International Energy Agency scenarios fall between these two SSPs (Schwalm et al, 2020). However, recent studies argue that SSP5-8.5 is unlikely (Hausfather and Peters, 2020), and current policies may rather lead to greenhouse gas emissions similar to those in SSP2-4.5 (Gillett, 2024). Accordingly, when only one SSP was considered, we chose SSP2-4.5 (Figures 4 and 5). In cases where both SSPs were used (Figures 1, 2 and 3), note that the uncertainty related to the 5 GCMs used is consistently higher than the SSP uncertainty.

For PHENOFIT, we extracted the following daily climate variables: minimum, mean and maximum daily temperatures, daily precipitation, daily global radiationdaily mean wind speed and daily relative humidity. We then computed the daily potential evapotranspiration with Penman–Monteith equation (FAO standard, Allen et al, 1998). Finally, for the correlative models, we used these daily variables to calculate the 4 climate predictors described above. Soil conditions (needed both for correlative and process-explicit models) were held constant throughout the simulations.

Uncertainty partitioning

Our approach was inspired by the partitioning of uncertainties in climate projections initially developed by Hawkins and Sutton (Hawkins and Sutton, 2009, 2011), which was subsequently enhanced with additional methodologies (e.g. Lafferty and Sriver, 2023; Yip et al, 2011). Rather than using a simple variance decomposition approach, we perform an ANOVA-based variance decomposition to also estimate the importance of the two-way interaction effects. All analyses were performed in R (R Core Team, 2024).

Across all species, we partitioned three sources of uncertainty: the climate projection uncertainty related to the different GCMs, SSPs, and their interaction, the species distribution modeling uncertainty related to the differents SDMs, and the species uncertainty related to the different species specific responses to climate change. We also considered the interactions between SDMs and climate projections (GCMs and SSPs), between SDMs and species, and between species and climate projections (Figure 1). For each year, the suitability of a cell was considered as a 21-year moving average suitability (e.g. 2040-2060 for the year 2050). We then computed the difference of suitability with the historical suitability (computed for each GCM on the period 1970-2000). For each GCM and each SSP, when multiple SDM projections were simulated within the same SDM approach (e.g. multiple inverse calibrations), we kept one ensemble per approach. For each year t, we then applied a linear ANOVA to calculate the sums of squares attributable to each uncertainty source:

$$SS_{tot} = SS_{GCM} + SS_{SSP} + SS_{GCM:SSP} + SS_{SDM} + SS_{SDM:GCM} + SS_{SDM:SSP}$$
$$+ SS_{species} + SS_{species:GCM} + SS_{species:SSP} + SS_{species:SDM} + SS_{residuals}$$

We then computed 90% uncertainty ranges additively and symmetrically around the mean projection (across all GCMs, SSPs, SDMs and species), e.g. for SDM uncertainty: $\pm 1.645 * \sigma * \frac{SS_{SDM}}{SS_{tot}}$ (Figure 1). Finally, we also partitioned the variance within each species. This implies applying the same ANOVA, but on species-level predictions, and thus dropping the species-related coefficients (Figure 3).

Results

The magnitude of uncertainties varied across ecoregions (Figure 1). In most Europe (Atlantic, Continental and Boreal), the 90% confidence interval encompassed a wide range of projected change in suitability (relative to the 1970-2000 reference period), and uncertainties increased significantly the further we get into the fu-

ture. In Mediterranean and Alpine ecoregions, the confidence interval was narrower and it increased much less with time (Figure 1). Despite these large uncertainties, trends could still be observed across Europe, along a Southwest to Northeast gradient (Figure 2A). For the 6 species considered here, the average projected suitability decreased in the Mediterranean Basin while it increased in the Boreal region as it could have been expected (Figures 1 and 2A). However, for the continental ecoregion, the trend was less clear and models showed the lowest agreement (Figure 2A).
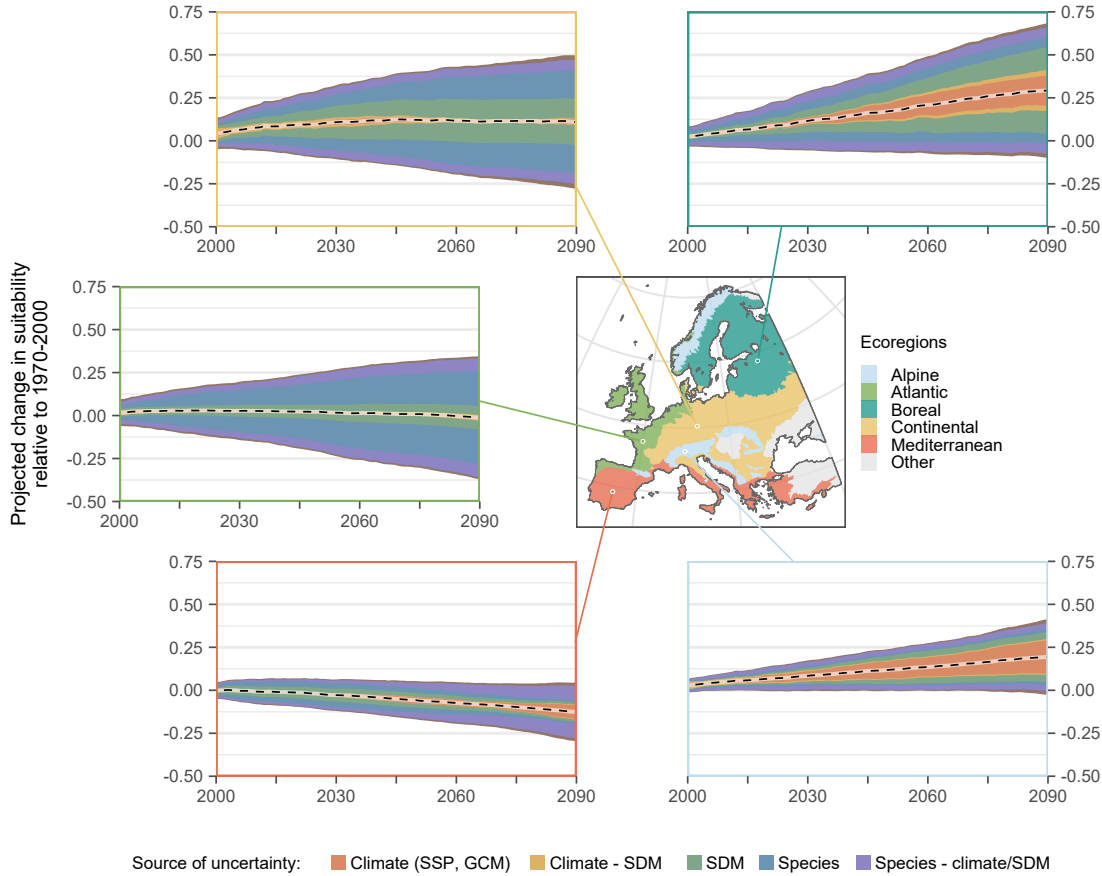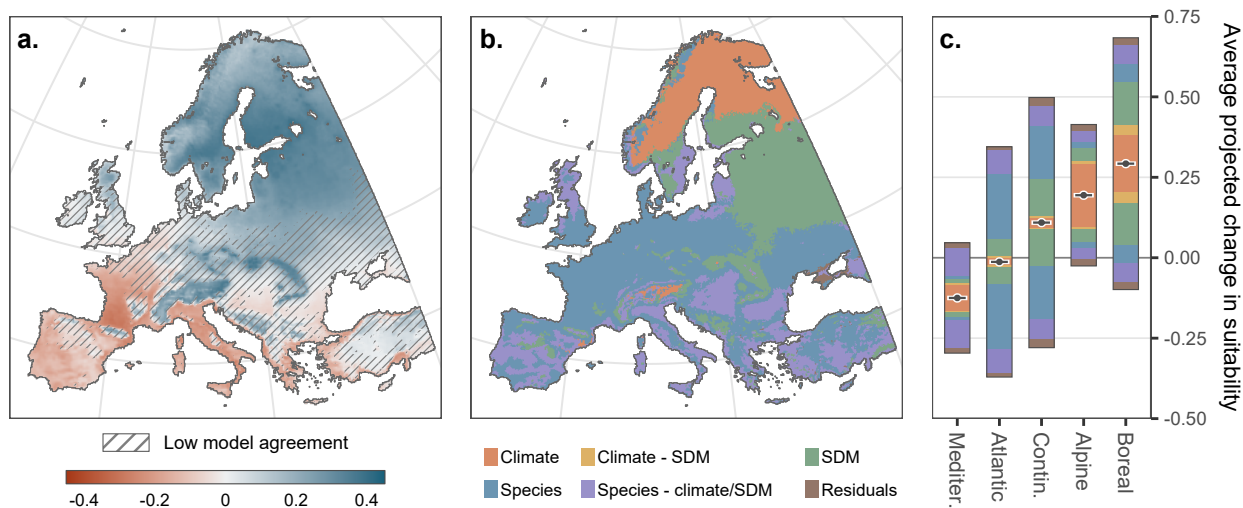

Figure 1: Evolution of climatic suitability change and variance partitioning across Europe's ecoregions. An ANOVA-based variance decomposition was performed to distinguish between 5 main uncertainty sources: (i) the future climate projections (GCM, SSP, and their interactions), (ii) the interactions between SDM approach and climate projections (both GCMs and SSPs), (iii) the SDM approach, (iv) the tree species, and (v) the interactions between species and both climate projections and SDM approaches. The dotted line represents the mean projection, across all GCMs, SSPs, SDMs and species. 90% uncertainty ranges were calculated additively and symmetrically around the mean.

The effects of the climate projections, the species and the modeling approach differed with respect to the ecoregion considered. Climate projection was the main source of uncertainty in the Alpine ecoregion, explaining 44% of total uncertainty in 2090 (Figures 1, 2B and 2C), while in the Atlantic and Continental ecoregions diferences between species responses was the main source of uncertainty (respectively 56.6% and 42.4% in 2090; Figures 2B and 2C). Interestingly, modelling approach was respectively the first and the second source of uncertainty in the Boreal (33.7%) and the Continental (29.4%) ecoregions (Figure 2C and **??**), which repre-

sent 58.6% of Europe total forest cover (**??**).

Two-way interactions between species and both climate projections and modeling approaches also represent a significant contribution to the total uncertainty (Figure 1). In 2090, they represent the major source of uncertainty in the Mediterranean ecoregion (50.1%; Figures 2B and 2C), and explain between 15.1% and 20.7% of the total uncertainty of the four other ecoregions. This stresses the importance of using ANOVAs to properly account for these interactions. In particular, the interaction between the species considered and the modelling approach is by far the most important factor (**??**), and reveals contrasted trends depending on the model and the species considered (**??**).


Figure 2: Projections of climatic suitability change and main source of uncertainty in 2090. (a) Overall change in fitness between the projection period 2080-2010 and the reference period 1970-2000, across all GCMs, SSPs, SDM approaches and species. Hashed shading reflects area where the three approaches of SDMs did not agree in the sign of suitability change. (b) Main source of uncertainty over the 2080-2100 period, according to a cell-based ANOVA partitioning. (c) Variance partitioning across Europe's ecoregions, for the 2080-2100 period. The black line represents the mean projection, across all GCMs, SSPs, SDMs and species. 90% uncertainty ranges were calculated additively and symmetrically around the mean.

At the species level, most uncertainty arises from the discrepancy between the projections of the different SDMs (Figure 3). Except for the Alpine region, SDM approach consistently represents the major source of uncertainty for the four other ecoregions (between 54.2% and 64.8%). For example, in the Continental ecoregion, differences across models account for 73.7% of the total uncertainty of beech future suitability, despite being within the core of its present distribution. Similarly, SDM is the main source of uncertainty for sessile and pedunculate oaks (respectively 57% and 76.8%, Figure 3). In Atlantic and Continental regions, the differences between species are strong: all models agreee with a lower suitability for fir and a higher suitability for holm and pubescent oaks, two Mediterranean species (Figure 3).

Our results also revealed that the divergent projections between SDM approaches followed a regular pattern. At the European scale, CSDM projections projected systematically stronger decrease in climatic suitability for all species than expert PEMs, especially in Mediterranean and Atlantic ecoregions and in the west-
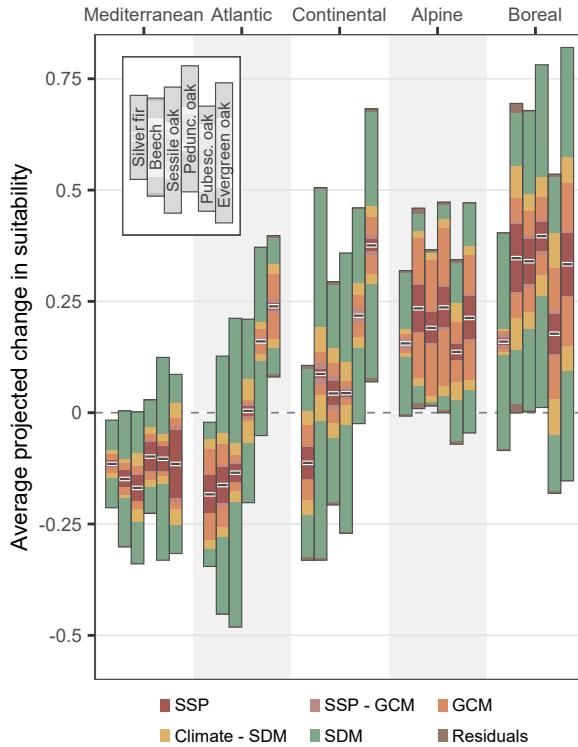
Figure 3: **Variance partitioning across Europe's ecoregions, for each species.** An ANOVA-based variance decomposition was performed to distinguish between 5 main uncertainty sources: (i) the future scenario (SSP), (ii) the climate model used to generate the climate projections (GCM), (iii) the interactions between the SPP and the GCM, (iv) the species distribution modeling method (SDM approach), and (v) the interactions between SDM approach and climate projections (both GCMs and SSPs). The black line represents the mean projection, across all GCMs, SSPs, SDMs and species. 90% uncertainty ranges were calculated additively and symmetrically around the mean. Inset plot shows the species name in the same order than in the main plot.

ern part of the Continental ecoregion (Figure 4 and **??????????**). Note the exception of holm oak for which the suitability decrease is more significant in the Mediterranean Basin according to PEM projections (though the average suitability across Europe remains more optimistic than other models, **??**). Overall, expert PEMs also simulated a higher increase of suitability in the transition zone between Continental and Boreal ecosystems. Fitted PEMs projections were closer to CSDM projections in the Southern and Western parts of Europe, i.e. the trailing edge of the range of most species, whereas they were closer to expert PEM ones in the North-West leading edge (Figure 4 and **??????????**). These discrepancies between modeling approaches can significantly change projected trends at the country level. In Germany for example, beech showed an average suitability decrease of -0.04 (± 0.09) in 2090 when considering only CSDM and fitted PEMs, i.e. the two SDM approaches entirely calibrated with current species distribution data, whereas the expert PEM simulated a suitability increase (0.39 ± 0.15). These discrepancies were also reflected in the simulated distribution for 2090 (Figure 5 and **??????????**). Beech did not show major extinction according to the expert PEM, whereas it was predicted to disappear from a large part of South-Western Europe by the CSDMs and the fitted PEMs (Figure 5). Partially fitted PEM projections were generally closer to expert PEM ones (Figure 4), but still simulate greater extinctions at the distribution limits of beech (Figure 5). Finally, disagreement between models within a model approach (area where less than 80% simulations show same sign of suitability change) varied geographically. For example, for beech, PEM projections mostly disagreed in Mediterranean and Atlantic ecoregions whereas CSDM simulations disagree in the eastern half of Europe (Figure 4).
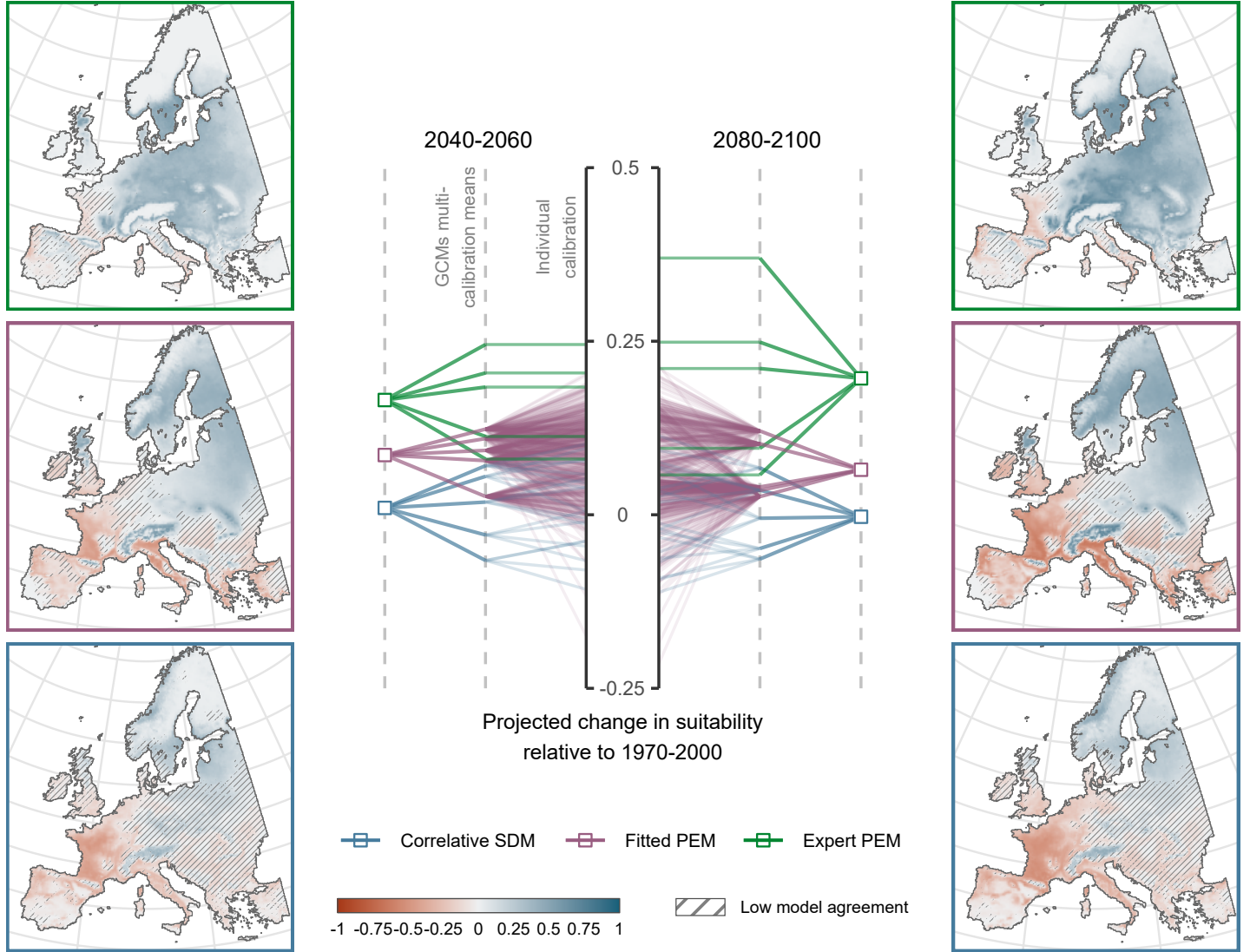
Figure 4: Discrepancies between model approaches in projected future climatic suitability change for beech. Models are forced with climatic data from 5 GCMs under scenario SSP2-4.5. Areas with a lack of model agreement (less than 80% of the individual calibrations agree on the sign of the change) are marked by hatching. Each individual calibrated model (i.e. 4 different CSDMs, 100 fitted PEM parameter sets, 10 partially fitted PEM parameter sets, and 1 expert PEM parameter set) was run with the 5 different GCM climatic variables (i.e. 20 CSDM projections, 500 fitted PEM projections, 50 part. fitted PEM projections, and 5 expert PEM projections). Then, they were averaged at the GCM-level within each SDM approach ("*GCMs multi-calibration means*"), and further averaged into one ensemble per SDM approach.

Discussion

Differences between model approaches generated high uncertainty in projected climatic suitability change. Across species, in a large part of Europe (Atlantic, Continental and Boreal ecoregions), discrepancies between modeling approaches are a more important source of uncertainty than the differences among climate model projections (GCMs) and socioeconomic scenarios (SSPs). In the Boreal ecoregion – where two very important forestry countries in terms of wood stock, added value, and forest-based workforce are located (Finland and Sweden) – SDM approaches are even a higher source of uncertainty (33.7% on average) than the difference across species (14.4%). In such notable case, it thus seems more critical to encompass the full model diversity rather than the full species diversity to get a comprehensive assessment of the magnitude of climatic suitability change. Note, however, that the models agree on more suitable climatic conditions in this region by the end of the 21st century (Figure 2A). At the species-level, the differences between modelling approaches is the main source of uncertainty for all the species considered here, and explain between 45% and 60% of the total uncertainty on average (Figure 3). One of the striking example is the climatic suitability change of sessile oak in the Atlantic region, where it represents an important cultural and economic value, and for which more than 80% of the uncertainty in climate change impact projections was due to variations among the different approaches of SDMs.

Previous studies had already shown that uncertainties within correlative models can be important (Thuiller et al, 2019). For example, in Wessely et al (2024), the proportion of species from the current European species pool that cannot be sustained throughout the century ranges from 24.5% (GLM) to 76.6% (Random Forest). Here we show that when considering a larger diversity of models, the total uncertainty in species climate suitability is even higher (Figure 3 and ??). Note in addition that we considered only one process-explicit model and focused on diverse approaches along the correlative-process continuum, but differences between process-explicit models can also be higher than differences between climate projections (Asseng et al, 2013). Ignoring the full diversity of models bias the estimation of other effects. For example, for beech, we would have estimated that discrepancies between GCMs would have been the major source of uncertainties (39.8%), higher than the SDM uncertainty (33.8%), whereas it was in reality much lower (18.8%) than SDM uncertainty (51.2%) when considering the three approaches of SDMs. Ignoring a large portion of uncertainty in species range projections due to modelling approaches can thus lead to overly confident predictions about which species will or will not be able to survive in future climates. This becomes increasingly true as we approach the end of the 21st century, where larger climate changes result in larger variation among projections (Figure 1).

CSDM and PEM future projections are known to diverge significantly (Cheaib et al, 2012; Keenan et al, 2011; Morin and Thuiller, 2009; Takolander et al, 2019). Here we show for the first time that the larger extinctions predicted in South-western Europe is associated to the method of calibration used. Indeed, the modeling

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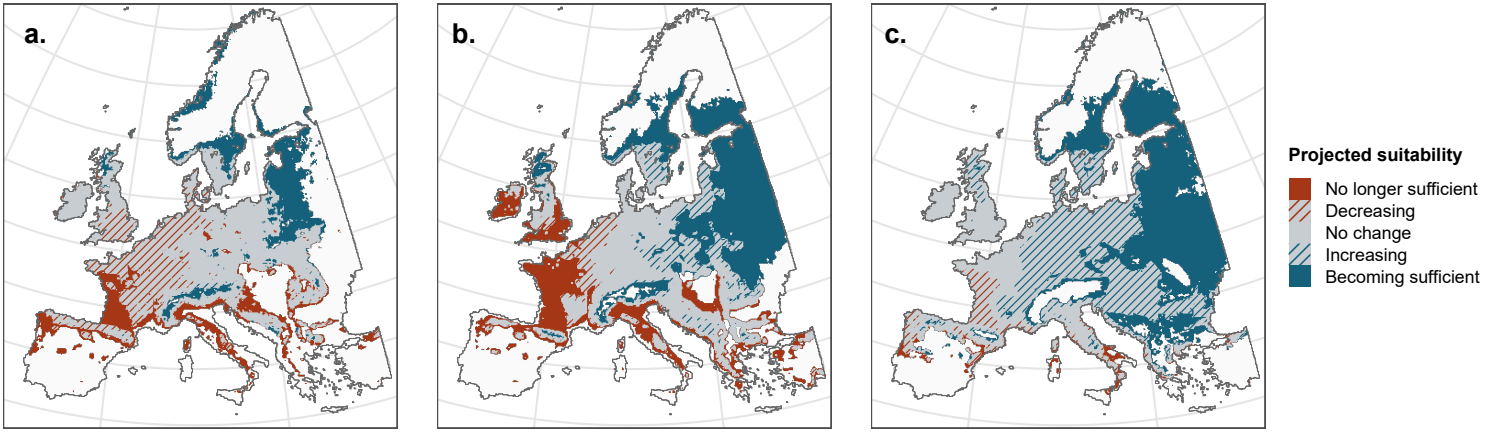
Figure 5: Projected beech distribution in 2090, according to (a) correlative species distribution models, (b) fitted process-explicit models, (c) partially fitted process-explicit models and (d) expert process-explicit models. Models are forced with climatic data from 5 GCMs under scenario SSP2-4.5. For each model approach, the species is considered present/absent if more than half of the simulations agree.

approaches – either statistical or process-explicit – that were fit to current species distribution data predict greater extinctions at the southern edge of species ranges than expert PEMs (Figure 5). Interestingly, we observed a gradient from correlative approaches fully determined by the current distribution to process-explicit approaches partially fitted with these data (Figure 4). Although we cannot determine which approach truly overestimates or underestimates future climatic threats (but see Van der Meersch et al, 2024; Chapter 2), we can hypothesize that distribution data are partly responsible for this pattern. This might be due to the fact that contemporary species occurrences are influenced by anthropogenic land use change which bias models calibration and may lead to smaller projected ranges (Ay et al, 2017; Faurby and Araújo, 2018). This bias may be partly removed by including past occurrences data (Faurby and Araújo, 2018), or by taking into account human-driven habitat modifications in the models (Ay et al, 2017). However, at the coarse scale of this study (0.1°), the bias may rather be due to the fact that recent distribution data do not cover the entire fundamental niche of the species, and thus that we underestimate the range of climatic conditions where species could survive (Chevalier et al, 2024; Nogués-Bravo et al, 2016). This fundamental niche truncation could be partly corrected by including paleorecords in the calibration process (Maiorano et al, 2013), but it may even increase the magnitude of projected future changes for some plants. For example, in Nogués-Bravo et al (2016), the genus *Fagus* shifted from a conservation status of "*Least Concerned*" to "*Endangered*" by 2050 in Europe when including such very long-term data. Another lever for improvement could be to consider local adaptation potential of species (Benito Garzón et al, 2011), as some populations may be pre-adapted to more challenging climatic conditions. In any case, including past distribution data or refining model with finer-scale data cannot prevent the issue of non-analogue future climatic conditions. Most paleorecords are limited to the Late Pleistocene/Holocene period (but see Chiarenza et al, 2023), i.e. to a cooler climate, and estimating the actual warm niche limits would require going back much further in time where paleorecords become even more challenging to use, and potentially where modern species did not yet exist (Burke et al, 2018; Chevalier

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et al, 2024). Process-explicit models are not concerned by bias in occurrence data when they are calibrated on experimental data – even though it can be also challenging to represent future climatic conditions in experiments (particularly extreme temperatures) – and may be more robust to novel climates (Van der Meersch et al, 2024; Chapter 2). In addition to fewer projected extinctions, PEMs, either expert or fitted, also projected more substantial range expansions towards the North and the East of Europe for most species considered here (consistently with other taxa, Buckley et al, 2010). Therefore, interestingly, fitted PEMs exhibited an intermediate behavior between CSDMs and expert PEMs: they lead to both larger extinctions in the South-Western part of Europe like CSDM and to larger climatic suitability increases in the North and Eastern part like expert PEMs. The constraints imposed by the structure of process-explicit models during the calibration may explain why they differ from correlative models, even though mathematical functions alone do not sufficiently constrain the calibration process (Chapter 3).

Beyond the differences between SDM approaches, multi-model projections are particularly useful for identifying general trends and guiding forest management. Such multi-model ensembles have been so far mostly restricted to statistical models (Simmonds et al, 2024), but we show here that there is a strong interest in considering a broader range of models to better characterize projections uncertainty. At the continental scale, it is possible to distinguish several regions that differ in terms of future climate risks and levers of action to address them (Figure 2). Around the Mediterranean Basin and in South-western France, the models agree in predicting generally less favorable climatic conditions for the species we considered here. In particular, the suitability of temperate broadleaf species (sessile and pedunculate oaks, beech) is projected to decrease while that of Mediterranean species (pubescent and evergreen oaks) is projected to increase. In some areas, evergreen oak has already replaced beech (Peñuelas and Boada, 2003). However, process-explicit model projections are more nuanced for deciduous oaks and beech in France, suggesting that some better-adapted populations will survive if the existing standing genetic variation is maintained and promoted by forest managers (Brang et al, 2014). On the contrary, the Scandinavian and Baltic countries, part of Poland and low mountain ranges of Central-Eastern Europe (Carpats, Ore Mountains, Sudetes) are projected to get an overall increase of climatic suitability. Thanks to a more favourable climate and an extended growing season, beech has been shown to be already more competitive at the northern margin of its range (Bolte et al, 2010), and could be favoured to convert pure coniferous stands into mixed forest in order to increase their resilience (Schauer et al, 2023). Climatic suitability is also projected to increase in the Alps and in the Scandinavian Mountains, but these areas are subject to a greater uncertainty related to climate projections (Figure 1), likely due to the more complex topography.

Large zones of Europe though exhibit less clear trends. There is a notable low agreement among models in the Continental ecoregion, which includes some countries with important forest sector (Germany, Romania...), as well as in the British Isles (except Scotland). In those regions, species-related uncertainty plays a major

role ([Figure 2A](#)) and indicates that one of the strategies to consider is the diversification of tree species, but also an increased genetic diversity within populations, to mitigate the risks associated with uncertain future conditions (Ammer, 2019; Morin et al, 2014; Pretzsch, 2021; Vospernik et al, 2024). Such unclear trends are also visible in the mountainous regions at the transition between Mediterranean and Continental/Atlantic climates (Pyrenees, Massif Central, Balkans). Finally, in some areas where most species are threatened, forest managers may consider introducing new species, more drought-tolerant. However, the lack of hindsight and experimental data often prevents the development and calibration of process-explicit models for such species.

We assessed uncertainties in species climatic suitability by quantifying the variance across the projections of a set of different models making the important hypothesis of equal likelihood of the projections of each model approach. As with climate models (IPCC, 2021), the spread in the projections could be reduced by weighting models according to their ability to reproduce past observations. A model's credibility is indeed increased if the model is able to simulate past species range shifts, especially under climatic conditions that significantly differ from the present ones. The ability to reproduce changes in tree distributions during large paleoclimate fluctuations is known to vary across the different approaches of species distribution modeling (Van der Meersch et al, 2024; Chapter 2). In particular, CSDMs showed less accurate predictions of species distribution change since the early Holocene (12,000 years ago) than process-explicit models (Van der Meersch et al, 2024; Chapter 2). Previous studies also pointed out that CSDMS projections for the coming decades would decline steadily in response to increasing climate novelty (Fitzpatrick et al, 2018). However, model evaluations using paleorecords may be biased by the sparse coverage in pollen data they used to infer past species distributions, and the magnitude and rate of future climate change will differ from the changes that occurred between the Last Glacial Maximum and today (the period for which most pollen records are available). It thus seem overly optimistic to summarize model discrepancies in one performance metric and then use it as the unique criteria in a model weighting scheme. Even when multivariate metrics are available, such as for climate models, there is no consensus that model weighting is more reliable than the "one-model-one-vote" strategy (IPCC, 2021).

Our results emphasise that it is critical to consider the diversity of modeling approaches that exist in order to ensure a consistent quantification of all model-related uncertainties in future species range shifts. Failure to fully quantify and report uncertainty, whether intentionally to preserve core messages, or not, leads to over-confidence in model projections (Simmonds et al, 2024), and may negatively impact public trust in scientists (Howe et al, 2019). To ensure the resilience and sustainability of Europe's forests, forest managers need to adopt adaptive management strategies that take account of all possible future conditions.

REFERENCES

Allen R, Pereira L, Raes D, Smith M (1998) Crop evapotranspiration: Guidelines for computing crop water requirements. FAO Irrigation and Drainage Papers 56

Ammer C (2019) Diversity and forest productivity in a changing climate. New Phytologist 221(1):50–66, DOI 10.1111/nph.15263, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/nph.15263

Asseng S, Ewert F, Rosenzweig C, Jones JW, Hatfield JL, Ruane AC, Boote KJ, Thorburn PJ, Rötter RP, Cammarano D, Brisson N, Basso B, Martre P, Aggarwal PK, Angulo C, Bertuzzi P, Biernath C, Challinor AJ, Doltra J, Gayler S, Goldberg R, Grant R, Heng L, Hooker J, Hunt LA, Ingwersen J, Izaurralde RC, Kersebaum KC, Müller C, Naresh Kumar S, Nendel C, O'Leary G, Olesen JE, Osborne TM, Palosuo T, Priesack E, Ripoche D, Semenov MA, Shcherbak I, Steduto P, Stöckle C, Stratonovitch P, Streck T, Supit I, Tao F, Travasso M, Waha K, Wallach D, White JW, Williams JR, Wolf J (2013) Uncertainty in simulating wheat yields under climate change. Nature Climate Change 3(9):827–832, DOI 10.1038/nclimate1916, URL https://www.nature.com/articles/nclimate1916

Ay JS, Guillemot J, Martin-StPaul N, Doyen L, Leadley P (2017) The economics of land use reveals a selection bias in tree species distribution models. Global Ecology and Biogeography 26(1):65–77, DOI 10.1111/geb.12514, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12514

Barbet-Massin M, Thuiller W, Jiguet F (2010) How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? Ecography 33(5):878–886, DOI 10.1111/j.1600-0587.2010.06181.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0587.2010.06181.x

Beaumont LJ, Pitman AJ, Poulsen M, Hughes L (2007) Where will species go? Incorporating new advances in climate modelling into projections of species distributions. Global Change Biology 13(7):1368–1385, DOI 10.1111/j.1365-2486.2007.01357.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2007.01357.x

Benito Garzón M, Alía R, Robson TM, Zavala MA (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. Global Ecology and Biogeography 20(5):766–778, DOI 10.1111/j.1466-8238.2010.00646.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1466-8238.2010.00646.x

Bolte A, Hilbrig L, Grundmann B, Kampf F, Brunet J, Roloff A (2010) Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce–beech forest. European Journal of Forest Research 129(3):261–276, DOI 10.1007/s10342-009-0323-1, URL https://doi.org/10.1007/s10342-009-0323-1

Brang P, Spathelf P, Larsen JB, Bauhus J, Boncčina A, Chauvin C, Drössler L, García-Güemes C, Heiri C, Kerr G, Lexer MJ, Mason B, Mohren F, Mühlethaler U, Nocentini S, Svoboda M (2014) Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry: An International Journal of Forest Research 87(4):492–503, DOI 10.1093/forestry/cpu018, URL https://doi.org/10.1093/forestry/cpu018

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? Ecology Letters 13(8):1041–1054, DOI 10.1111/j.1461-0248.2010.01479.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2010.01479.x

Burke KD, Williams JW, Chandler MA, Haywood AM, Lunt DJ, Otto-Bliesner BL (2018) Pliocene and Eocene provide best analogs for near-future climates. Proceedings of the National Academy of Sciences 115(52):13288–13293, DOI 10.1073/pnas.1809600115, URL https://www.pnas.org/content/115/52/13288

Carnicer J, Alegria A, Giannakopoulos C, Di Giuseppe F, Karali A, Koutsias N, Lionello P, Parrington M, Vitolo C (2022) Global warming is shifting the relationships between fire weather and realized fire-induced CO2 emissions in Europe. Scientific Reports 12(1):10365, DOI 10.1038/s41598-022-14480-8, URL https://www.nature.com/articles/s41598-022-14480-8

Cheaib A, Badeau V, Boe J, Chuine I, Delire C, Dufrêne E, François C, Gritti ES, Legay M, Pagé C, Thuiller W, Viovy N, Leadley P (2012) Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecology Letters 15(6):533–544, DOI 10.1111/j.1461-0248.2012.01764.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2012.01764.x

Chen G, Kéry M, Plattner M, Ma K, Gardner B (2013) Imperfect detection is the rule rather than the exception in plant distribution studies. Journal of Ecology 101(1):183–191, DOI 10.1111/1365-2745.12021, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2745.12021

Chevalier M, Broennimann O, Guisan A (2024) Climate change may reveal currently unavailable parts of species' ecological niches. Nature Ecology & Evolution pp 1–13, DOI 10.1038/s41559-024-02426-4, URL https://www.nature.com/articles/s41559-024-02426-4

Chiarenza AA, Waterson AM, Schmidt DN, Valdes PJ, Yesson C, Holroyd PA, Collinson ME, Farnsworth A, Nicholson DB, Varela S, Barrett PM (2023) 100 million years of turtle paleoniche dynamics enable the prediction of latitudinal range shifts in a warming world. Current Biology 33(1):109–121.e3, DOI 10.1016/j.cub.2022.11.056, URL https://www.sciencedirect.com/science/article/pii/S0960982222018474

Cienciala E, Melichar J (2024) Forest carbon stock development following extreme drought-induced dieback of coniferous stands in Central Europe: a CBM-CFS3 model application. Carbon Balance and Management 19(1):1, DOI 10.1186/s13021-023-00246-w, URL https://doi.org/10.1186/s13021-023-00246-w

Copernicus Climate Change Service (2024) European state of the climate 2023. Tech. rep., DOI 10.24381/BS9V-8C66, URL https://climate.copernicus.eu/esotc/2023

Diniz-Filho JAF, Mauricio Bini L, Fernando Rangel T, Loyola RD, Hof C, Nogués-Bravo D, Araújo MB (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography 32(6):897–906, DOI 10.1111/j.1600-0587.2009.06196.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0587.2009.06196.x

Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2012) Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography 39(12):2119–2131, DOI 10.1111/j.1365-2699.2011.02659.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2699.2011.02659.x

Dunne JP, Horowitz LW, Adcroft AJ, Ginoux P, Held IM, John JG, Krasting JP, Malyshev S, Naik V, Paulot F, Shevliakova E, Stock CA, Zadeh N, Balaji V, Blanton C, Dunne KA, Dupuis C, Durachta J, Dussin R, Gauthier PPG, Griffies SM, Guo H, Hallberg RW, Harrison M, He J, Hurlin W, McHugh C, Menzel R, Milly PCD, Nikonov S, Paynter DJ, Ploshay J, Radhakrishnan A, Rand K, Reichl BG, Robinson T, Schwarzkopf DM, Sentman LT, Underwood S, Vahlenkamp H, Winton M, Wittenberg AT, Wyman B, Zeng Y, Zhao M (2020) The GFDL Earth System Model Version 4.1 (GFDL-ESM 4.1): Overall Coupled Model Description and Simulation Characteristics. Journal of Advances in Modeling Earth Systems 12(11):e2019MS002015, DOI 10.1029/2019MS002015, URL https://onlinelibrary.wiley.com/doi/abs/10.1029/2019MS002015

Duputié A, Zimmermann NE, Chuine I (2014) Where are the wild things? why we need better data on species distribution. Global Ecology and Biogeography 23:457–467, DOI 10.1111/geb.12118

Duputié A, Rutschmann A, Ronce O, Chuine I (2015) Phenological plasticity will not help all species adapt to climate change.

Global Change Biology 21(8):3062–3073, DOI 10.1111/gcb.12914, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12914

Dyderski MK, Paz S, Frelich LE, Jagodzinski AM (2018) How much does climate change threaten European forest tree species distributions? Global Change Biology 24(3):1150–1163, DOI 10.1111/gcb.13925, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13925

Faurby S, Araújo MB (2018) Anthropogenic range contractions bias species climate change forecasts. Nature Climate Change 8(3):252–256, DOI 10.1038/s41558-018-0089-x, URL https://www.nature.com/articles/s41558-018-0089-x

Fitzpatrick MC, Blois JL, Williams JW, Nieto-Lugilde D, Maguire KC, Lorenz DJ (2018) How will climate novelty influence ecological forecasts? Using the Quaternary to assess future reliability. Global Change Biology 24(8):3575–3586, DOI 10.1111/gcb.14138, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14138

Gauzere J, Teuf B, Davi H, Chevin LM, Caignard T, Leys B, Delzon S, Ronce O, Chuine I (2020) Where is the optimum? Predicting the variation of selection along climatic gradients and the adaptive value of plasticity. A case study on tree phenology. Evolution Letters 4(2):109–123, DOI 10.1002/evl3.160, URL https://onlinelibrary.wiley.com/doi/abs/10.1002/evl3.160

Gillett NP (2024) Halving of the uncertainty in projected warming over the past decade. npj Climate and Atmospheric Science 7(1):1–3, DOI 10.1038/s41612-024-00693-3, URL https://www.nature.com/articles/s41612-024-00693-3

Hadden D, Grelle A (2016) Changing temperature response of respiration turns boreal forest from carbon sink into carbon source. Agricultural and Forest Meteorology 223:30–38, DOI 10.1016/j.agrformet.2016.03.020, URL https://www.sciencedirect.com/science/article/pii/S0168192316302131

Hanewinkel M, Cullmann DA, Schelhaas MJ, Nabuurs GJ, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change 3(3):203–207, DOI 10.1038/nclimate1687, URL https://www.nature.com/articles/nclimate1687

Hansen N, Ostermeier A (2001) Completely Derandomized Self-Adaptation in Evolution Strategies. Evolutionary Computation 9(2):159–195, DOI 10.1162/106365601750190398

Hausfather Z, Peters GP (2020) Emissions – the 'business as usual' story is misleading. Nature 577(7792):618–620, DOI 10.1038/d41586-020-00177-3, URL https://www.nature.com/articles/d41586-020-00177-3

Hawkins E, Sutton R (2009) The Potential to Narrow Uncertainty in Regional Climate Predictions. Bulletin of the American Meteorological Society 90(8):1095–1108, DOI 10.1175/2009BAMS2607.1, URL https://journals.ametsoc.org/view/journals/bams/90/8/2009bams2607_1.xml

Hawkins E, Sutton R (2011) The potential to narrow uncertainty in projections of regional precipitation change. Climate Dynamics 37(1):407–418, DOI 10.1007/s00382-010-0810-6, URL https://doi.org/10.1007/s00382-010-0810-6

Hengl T, Jesus JMd, Heuvelink GBM, Gonzalez MR, Kilibarda M, Blagotic A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B, Guevara MA, Vargas R, MacMillan RA, Batjes NH, Leenaars JGB, Ribeiro E, Wheeler I, Mantel S, Kempen B (2017) SoilGrids250m: Global gridded soil information based on machine learning. PLOS ONE 12(2):e0169748, DOI 10.1371/journal.pone.0169748, URL https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0169748

Hickler T, Vohland K, Feehan J, Miller PA, Smith B, Costa L, Giesecke T, Fronzek S, Carter TR, Cramer W, Kühn I, Sykes MT (2012) Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography 21(1):50–63, DOI 10.1111/j.1466-8238.2010.00613.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1466-8238.2010.00613.x

Howe LC, MacInnis B, Krosnick JA, Markowitz EM, Socolow R (2019) Acknowledging uncertainty impacts public acceptance of climate scientists' predictions. Nature Climate Change 9(11):863–867, DOI 10.1038/s41558-019-0587-5, URL https://www.nature.com/articles/s41558-019-0587-5

Hyyrynen M, Ollikainen M, Seppälä J (2023) European forest sinks and climate targets: past trends, main drivers, and future forecasts. European Journal of Forest Research 142(5):1207–1224, DOI 10.1007/s10342-023-01587-4, URL https://doi.org/10.1007/s10342-023-01587-4

IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, DOI 10.1017/9781009157896, URL https://report.ipcc.ch/ar6/wg1/IPCC_AR6_WGI_FullReport.pdf

Karelin DV, Zamolodchikov DG, Shilkin AV, Popov SY, Kumanyaev AS, de Gerenyu VOL, Tel'nova NO, Gitarskiy ML (2021) The effect of tree mortality on CO2 fluxes in an old-growth spruce forest. European Journal of Forest Research 140(2):287–305, DOI 10.1007/s10342-020-01330-3, URL https://doi.org/10.1007/s10342-020-01330-3

Keenan T, Maria Serra J, Lloret F, Ninyerola M, Sabate S (2011) Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters! Global Change Biology 17(1):565–579, DOI 10.1111/j.1365-2486.2010.02254.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2010.02254.x

Kelly J, Kljun N, Cai Z, Doerr SH, D'Onofrio C, Holst T, Lehner I, Lindroth A, Thapa S, Vestin P, Santín C (2024) Wildfire impacts on the carbon budget of a managed Nordic boreal forest. Agricultural and Forest Meteorology 351:110016, DOI 10.1016/j.agrformet.2024.110016, URL https://www.sciencedirect.com/science/article/pii/S016819232400131X

Korosuo A, Pilli R, Abad Viñas R, Blujdea VNB, Colditz RR, Fiorese G, Rossi S, Vizzarri M, Grassi G (2023) The role of forests in the EU climate policy: are we on the right track? Carbon Balance and Management 18(1):15, DOI 10.1186/s13021-023-00234-0, URL https://doi.org/10.1186/s13021-023-00234-0

Lafferty DC, Sriver RL (2023) Downscaling and bias-correction contribute considerable uncertainty to local climate projections in CMIP6. npj Climate and Atmospheric Science 6(1):1–13, DOI 10.1038/s41612-023-00486-0, URL https://www.nature.com/articles/s41612-023-00486-0

Latifovic L, Arain MA (2024) The impact of spongy moth (*Lymantria dispar dispar*) defoliation on carbon balance of a temperate deciduous forest in North America. Agricultural and Forest Meteorology 354:110076, DOI 10.1016/j.agrformet.2024.110076, URL https://www.sciencedirect.com/science/article/pii/S0168192324001916

Levins R (1993) A Response to Orzack and Sober: Formal Analysis and the Fluidity of Science. The Quarterly Review of Biology 68(4):547–555, DOI 10.1086/418302, URL https://www.journals.uchicago.edu/doi/abs/10.1086/418302

Lurton T, Balkanski Y, Bastrikov V, Bekki S, Bopp L, Braconnot P, Brockmann P, Cadule P, Contoux C, Cozic A, Cugnet D, Dufresne JL, Éthé C, Foujols MA, Ghattas J, Hauglustaine D, Hu RM, Kageyama M, Khodri M, Lebas N, Levavasseur G, Marchand M, Ottlé C, Peylin P, Sima A, Szopa S, Thiéblemont R, Vuichard N, Boucher O (2020) Implementation of the CMIP6 Forcing Data in the IPSL-CM6A-LR Model. Journal of Advances in Modeling Earth Systems 12(4):e2019MS001940, DOI 10.1029/2019MS001940, URL https://onlinelibrary.wiley.com/doi/abs/10.1029/2019MS001940

Maiorano L, Cheddadi R, Zimmermann NE, Pellissier L, Petitpierre B, Pottier J, Laborde H, Hurdu BI, Pearman PB, Psomas A, Singarayer JS, Broennimann O, Vittoz P, Dubuis A, Edwards ME, Binney HA, Guisan A (2013) Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. Global Ecology and Biogeography 22(3):302–317, DOI 10.1111/j.1466-8238.2012.00767.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1466-8238.2012.00767.x

Mauri A, Strona G, San-Miguel-Ayanz J (2017) EU-Forest, a high-resolution tree occurrence dataset for Europe. Scientific Data 4(1):160123, DOI 10.1038/sdata.2016.123, URL https://www.nature.com/articles/sdata2016123

Van der Meersch V, Chuine I (2023) Estimating process-based model parameters from species distribution data using the evolutionary algorithm CMA-ES. Methods in Ecology and Evolution 14(7):1808–1820, DOI 10.1111/2041-210X.14119, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.14119

Van der Meersch V, Armstrong E, Mouillot F, Duputié A, Davi H, Saltré F, Chuine I (2024) Biological mechanisms are necessary to improve projections of species range shifts. bioRxiv DOI 10.1101/2024.05.06.592679, URL https://www.biorxiv.org/content/early/2024/05/08/2024.05.06.592679, https://www.biorxiv.org/content/early/2024/05/08/2024.05.06.592679.full.pdf

Mitchell S, Dietrich M (2006) Integration without Unification: An Argument for Pluralism in the Biological Sciences. The American Naturalist 168(S6):S73–S79, DOI 10.1086/509050, URL https://www-journals-uchicago-edu.inee.bib.cnrs.fr/doi/10.1086/509050

Morin X, Thuiller W (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90(5):1301–1313, DOI 10.1890/08-0134.1, URL https://onlinelibrary.wiley.com/doi/abs/10.1890/08-0134.1

Morin X, Augspurger C, Chuine I (2007) Process-Based Modeling of Species' Distributions: What Limits Temperate Tree Species' Range Boundaries? Ecology 88(9):2280–2291, DOI 10.1890/06-1591.1, URL https://onlinelibrary.wiley.com/doi/abs/10.1890/06-1591.1

Morin X, Fahse L, de Mazancourt C, Scherer-Lorenzen M, Bugmann H (2014) Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. Ecology Letters 17(12):1526–1535, DOI 10.1111/ele.12357, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12357

Muñoz-Sabater J, Dutra E, Agustí-Panareda A, Albergel C, Arduini G, Balsamo G, Boussetta S, Choulga M, Harrigan S, Hersbach H (2021) ERA5-Land: A state-of-the-art global reanalysis dataset for land applications. Earth system science data 13(9):4349–4383

Müller WA, Jungclaus JH, Mauritsen T, Baehr J, Bittner M, Budich R, Bunzel F, Esch M, Ghosh R, Haak H, Ilyina T, Kleine T, Kornblueh L, Li H, Modali K, Notz D, Pohlmann H, Roeckner E, Stemmler I, Tian F, Marotzke J (2018) A Higher-resolution Version of the Max Planck Institute Earth System Model (MPI-ESM1.2-HR). Journal of Advances in Modeling Earth Systems 10(7):1383–1413, DOI 10.1029/2017MS001217, URL https://onlinelibrary.wiley.com/doi/abs/10.1029/2017MS001217

Nogués-Bravo D, Veloz S, Holt BG, Singarayer J, Valdes P, Davis B, Brewer SC, Williams JW, Rahbek C (2016) Amplified plant turnover in response to climate change forecast by Late Quaternary records. Nature Climate Change 6(12):1115–1119, DOI 10.1038/nclimate3146, URL https://www.nature.com/articles/nclimate3146

Noël T, Loukos H, Defrance D, Vrac M, Levavasseur G (2022) Extending the global high-resolution downscaled projections dataset to include CMIP6 projections at increased resolution coherent with the ERA5-Land reanalysis. Data in Brief 45:108669, DOI 10.1016/j.dib.2022.108669, URL https://www.sciencedirect.com/science/article/pii/S2352340922008745

Ohlemüller R, Gritti ES, Sykes MT, Thomas CD (2006) Quantifying components of risk for European woody species under climate change. Global Change Biology 12(9):1788–1799, DOI 10.1111/j.1365-2486.2006.01231.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2006.01231.x

Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. Journal of Biogeography 33(10):1704–1711, DOI 10.1111/j.1365-2699.2006.01460.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2699.2006.01460.x

Petchey OL, Pontarp M, Massie TM, Kéfi S, Ozgul A, Weilenmann M, Palamara GM, Altermatt F, Matthews B, Levine JM, Childs DZ, McGill BJ, Schaepman ME, Schmid B, Spaak P, Beckerman AP, Pennekamp F, Pearse IS (2015) The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters 18(7):597–611, DOI 10.1111/ele.12443, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12443

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology 9(2):131–140, DOI 10.1046/j.1365-2486.2003.00566.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2003.00566.x

Pretzsch H (2021) Genetic diversity reduces competition and increases tree growth on a Norway spruce (*Picea abies* [L.] Karst.) provenance mixing experiment. Forest Ecology and Management 497:119498, DOI 10.1016/j.foreco.2021.119498, URL https://www.sciencedirect.com/science/article/pii/S0378112721005880

R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL https://www.R-project.org/

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40(8):913–929, DOI 10.1111/ecog.02881, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.02881

Saltré F, Saint-Amant R, Gritti ES, Brewer S, Gaucherel C, Davis BAS, Chuine I (2013) Climate or migration: what limited European beech post-glacial colonization? Global Ecology and Biogeography 22(11):1217–1227, DOI 10.1111/geb.12085, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12085

Saltré F, Duputié A, Gaucherel C, Chuine I (2015) How climate, migration ability and habitat fragmentation affect the projected future distribution of European beech. Global Change Biology 21(2):897–910, DOI 10.1111/gcb.12771, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12771

Schauer B, Thorn S, Blaschke M, Kudernatsch T (2023) Conversion of pure spruce to mixed spruce beech stands: Effects on alpha and beta diversity of multiple taxonomic groups. Forest Ecology and Management 545:121297, DOI 10.1016/j.foreco.2023.121297, URL https://www.sciencedirect.com/science/article/pii/S0378112723005315

Schueler S, Falk W, Koskela J, Lefèvre F, Bozzano M, Hubert J, Kraigher H, Longauer R, Olrik DC (2014) Vulnerability of dynamic genetic conservation units of forest trees in Europe to climate change. Global Change Biology 20(5):1498–1511, DOI 10.1111/gcb.12476, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12476

Schwalm CR, Glendon S, Duffy PB (2020) Rcp8.5 tracks cumulative co2 emissions. Proceedings of the National Academy of Sciences 117(33):19656–19657, DOI 10.1073/pnas.2007117117

Sellar AA, Walton J, Jones CG, Wood R, Abraham NL, Andrejczuk M, Andrews MB, Andrews T, Archibald AT, de Mora L, Dyson H, Elkington M, Ellis R, Florek P, Good P, Gohar L, Haddad S, Hardiman SC, Hogan E, Iwi A, Jones CD, Johnson B, Kelley DI, Kettleborough J, Knight JR, Köhler MO, Kuhlbrodt T, Liddicoat S, Linova-Pavlova I, Mizielinski MS, Morgenstern O, Mulcahy J, Neininger E, O'Connor FM, Petrie R, Ridley J, Rioual JC, Roberts M, Robertson E, Rumbold S, Seddon J, Shepherd H, Shim S, Stephens CM, Teixiera JC, Tang Y, Williams J, Wiltshire A, Griffiths PT (2020) Implementation of U.K. Earth System Models for CMIP6. Journal of Advances in Modeling Earth Systems 12(4):e2019MS001946, DOI 10.1029/2019MS001946, URL https://onlinelibrary.wiley.com/doi/abs/10.1029/2019MS001946

Senf C, Buras A, Zang CS, Rammig A, Seidl R (2020) Excess forest mortality is consistently linked to drought across Europe. Nature Communications 11(1):6200, DOI 10.1038/s41467-020-19924-1, URL https://www.nature.com/articles/s41467-020-19924-1

Simmonds EG, Adjei KP, Cretois B, Dickel L, González-Gil R, Laverick JH, Mandeville CP, Mandeville EG, Ovaskainen O, Sicacha-Parada J, Skarstein ES, O'Hara B (2024) Recommendations for quantitative uncertainty consideration in ecology and evolution. Trends in Ecology & Evolution 39(4):328–337, DOI 10.1016/j.tree.2023.10.012, URL https://www.sciencedirect.com/science/article/pii/S0169534723002793

Takolander A, Hickler T, Meller L, Cabeza M (2019) Comparing future shifts in tree species distributions across Europe projected by statistical and dynamic process-based models. Regional Environmental Change 19(1):251–266, DOI 10.1007/s10113-018-1403-x, URL https://doi.org/10.1007/s10113-018-1403-x

Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE (2019) Uncertainty in ensembles of global biodiversity scenarios. Nature Communications 10(1):1446, DOI 10.1038/s41467-019-09519-w, URL https://www.nature.com/articles/s41467-019-09519-w

Tóth B, Weynants M, Pásztor L, Hengl T (2017) 3D soil hydraulic database of Europe at 250 m resolution. Hydrological Processes 31(14):2662–2666, DOI 10.1002/hyp.11203, URL https://onlinelibrary.wiley.com/doi/abs/10.1002/hyp.11203

Urban MC, Bocedi G, Hendry AP, Mihoub JB, Pe'er G, Singer A, Bridle JR, Crozier LG, De Meester L, Godsoe W, Gonzalez A, Hellmann JJ, Holt RD, Huth A, Johst K, Krug CB, Leadley PW, Palmer SCF, Pantel JH, Schmitz A, Zollner PA, Travis JMJ (2016) Improving the forecast for biodiversity under climate change. Science 353(6304):aad8466, DOI 10.1126/science.aad8466, URL https://www.science.org/doi/10.1126/science.aad8466

Valavi R, Guillera-Arroita G, Lahoz-Monfort JJ, Elith J (2022) Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. Ecological Monographs 92(1):e01486, DOI 10.1002/ecm.1486, URL https://onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1486

Vospernik S, Vigren C, Morin X, Toïgo M, Bielak K, Brazaitis G, Bravo F, Heym M, del Río M, Jansons A, Löf M, Nothdurft A, Pardos M, Pach M, Ponette Q, Pretzsch H (2024) Can mixing *Quercus robur* and *Quercus petraea* with *Pinus sylvestris* compensate for productivity losses due to climate change? Science of The Total Environment 942:173342, DOI 10.1016/j.scitotenv.2024.173342, URL https://www.sciencedirect.com/science/article/pii/S0048969724034892

Wessely J, Essl F, Fiedler K, Gattringer A, Hülber B, Ignateva O, Moser D, Rammer W, Dullinger S, Seidl R (2024) A climate-induced tree species bottleneck for forest management in Europe. Nature Ecology & Evolution 8(6):1109–1117, DOI 10.1038/s41559-024-02406-8, URL https://www-nature-com.inee.bib.cnrs.fr/articles/s41559-024-02406-8

van der Woude AM, Peters W, Joetzjer E, Lafont S, Koren G, Ciais P, Ramonet M, Xu Y, Bastos A, Botía S, Sitch S, de Kok R, Kneuer T, Kubistin D, Jacotot A, Loubet B, Herig-Coimbra PH, Loustau D, Luijkx IT (2023) Temperature extremes of 2022 reduced carbon uptake by forests in Europe. Nature Communications 14(1):6218, DOI 10.1038/s41467-023-41851-0, URL https://www.nature.com/articles/s41467-023-41851-0

Yip S, Ferro CAT, Stephenson DB, Hawkins E (2011) A Simple, Coherent Framework for Partitioning Uncertainty in Climate Predictions. Journal of Climate 24(17):4634–4643, DOI 10.1175/2011JCLI4085.1, URL https://journals.ametsoc.org/view/journals/clim/24/17/2011jcli4085.1.xml

Yukimoto S, Kawai H, Koshiro T, Oshima N, Yoshida K, Urakawa S, Tusjino H, Deushi M, Tanaka T, Hosaka M, Yabu S, Yoshimura H, Shindo E, Mizuta R, Obata A, Adachi Y, Ishii M (2019) The meteorological research institute earth system model version 2.0, mri-esm2.0: Description and basic evaluation of the physical component. Journal of the Meteorological Society of Japan Ser II 97(5):931–965, DOI 10.2151/jmsj.2019-051